Effects of Controlled SO_2 Exposure on Net Primary Production and Plant Biomass Dynamics

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Abstract

Objectives of this study were to determine effects of low level SO_2 fumigation on above- and belowground plant biomass dynamics and aboveground net primary production. With two exceptions we were unable to measure significant effects on these parameters. Rates of increase in rhizome biomass over the 4-year period of the study were reduced by SO_2 and indicate that long-term exposure of this grassland to low level SO_2 may ultimately reduce the vigor of the perennating organs to a point where above- and belowground biomass dynamics will be altered, net primary production will be reduced, and species composition will be modified. In addition, production of *Bromus japonicus*, a cool-season annual grass, was reduced by SO_2 fumigation.

Because of the increase in electrical power production in the northern Great Plains, air pollution (particularly SO_2) is expected to increase (Northern Great Plains Resource Program, 1975). Aside from mining and power generation, the main economic activity of the region is range livestock production. It is quite possible that altered air quality will affect the livestock industry. Northern Great Plains rangelands are native ecosystems that are complex combinations of indigenous plant and animal species that interact with each other and their physical environment in capturing, storing, and utilizing energy in a self-sustaining manner. Under normal circumstances, domestic livestock production can be fit into this process quite profitably without interfering with the self-sustaining character of the ecosystem processes (Lewis 1969). Further, livestock production on rangelands is closely associated with the quantity and quality of aboveground forage production. The threat that air pollution poses to a livestock industry based on native rangeland is threefold: direct effect of air pollutants on the livestock, direct effect on quantity and quality of forage production, and effects on the self-sustaining properties of the ecosystem. The last two of these questions are considered for one grassland type in this study.

Several investigators have reported biomass dynamics and net primary production estimates for the northern mixed grass prairie under pollution-free conditions (Coupland 1973; Lauenroth and Whitman 1977; Lauenroth et al. 1975; Dodd et al. 1974). These studies indicate rapid increases of plant biomass in late May, June, and early July and aboveground net primary productivity estimates ranging from 100 to 200 $g \bullet m^{-2} \bullet yr^{-1}$. Although the species composition of these grasslands is dependent on factors, such as soils, rainfall, and grazing history, these grasslands are nearly always dominated by cool-season grass species, and in most cases *Agropyron smithii* Rydb. is the main species.

Although much research has been done on effects of air pollution on plants of ornamental or agronomic importance (see reviews by Daines 1968; Mudd and Kozlowski 1975; Treshow 1970), comparatively little has been conducted on effects on productivity of the native plant species of the semiarid rangelands of the western United States. Recent studies indicate that grasses of semiarid rangelands are more resistant to air pollution than are agronomic species (Hill et al. 1974, Bennet and Hill 1973, Davis et al. 1966, Tingey et al. 1976). However, Ferenbaugh (1977) reported deleterious effects of SO_2 at concentrations as low as 0.13 ppm on production of *Oryzopsis hymenoides,* a native cool-season grass found in semiarid climates of the western United States.

The objectives of this study were to determine the short- and near-term effects of exposure to low level SO_2 concentration on biomass dynamics and aboveground net primary productivity (ANPP) of a northern mixed grass prairie. We hypothesized that low level exposure of SO_2 throughout the growing season would reduce ANPP and change species and species group contributions to total ANPP.

Study Areas

The study areas (Site I and Site II) were located in southeast Montana in the Fort Howes District of Custer National Forest (45° 15′N, 106° E). Site II was located 1 km southeast of Site I and both were on rolling upland sites with southwest-facing slopes of less than 4°. The soils of both sites were formed from parent materials deposited as outwash from nearby buttes and ridges (Soil Conservation Service, 1971). Site I is located on a Farland silty clay loam and Site II is on a Thurlow clay loam (Dodd et al. 1978). Both soil series have well developed A and B horizons with solums extending to $\cong$ 100 cm. Both sites had previously been subjected to moderate cattle grazing in summer and fall. Range condition was estimated as good for all plots on Site 1 in 1974 (Taylor et al., 1976). A grazing pressure gradient was evident among the plots of Site II. Before fencing in the fall of 1975, range condition varied from poor on the control area to good on the high SO_2 treatment plot.

The local climate is continental, semiarid, and extremely variable (Riley and Spolton 1974). Approximately 50% of the annual precipitation (approximately 360 mm) is received in April, May, and June, with less than 20% received between December and March (National Oceanic and Atmospheric Administration, 1976). July, the warmest month, has an average temperature of 22° C, while January, the coldest month, has an average temperature of -8° C. Differences between daytime maximum and nighttime minimum temperatures during July and August often exceed 25° C. Normally, the frost-free growing season lasts approximately 130 days and begins near mid-May (Brown 1971).

The vegetation of the region is a ponderosa pine (*Pinus ponderosa* Laws.) grassland complex (Kuchler 1964; Payne 1973; Ross and Hunter 1976). Vegetation on the uplands is classified as northern mixed grass prairie (Brown 1971) with open stands of pine restricted to steeper slopes of buttes and canyons. A heavy understory of mid-grasses is associated with the pine stands. Western wheatgrass, the dominant species on both sites, is a cool-season

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species and has the C_3 photosynthetic pathway (Williams 1973). Grass species of secondary importance on the sites were prairie junegrass (*Koeleria cristata* L.); Sandberg bluegrass (*Poa secunda* Presl.); Kentucky bluegrass (*P. pratensis* L.); needle-and-thread (*Stipa comata* Trin. and Ruper); green needlegrass (*S. viridula* Trin.); and Japanese brome (*Bromus japonicus* Thurb.). Major forbs were: western yarrow (*Achillea millefolium* L.); common dandelion (*Taraxacum officinale* Weber); and goatsbeard (*Tragopogon dubuis* Scop.). Fringed sagewort (*Artemisia frigida* Willd.) was the major half-shrub.

Materials and Methods

Plots (0.52 ha) on the two study sites were continuously fumigated throughout the growing season at geometric mean SO_2 concentrations of $<26\ \mu g \cdot m^{-3}$ (control), $60\ \mu g \cdot m^{-3}$ (low treatment), $105\ \mu g \cdot m^{-3}$ (medium treatment) and $180\ \mu g \cdot m^{-3}$ (high treatment) (Preston and Gullett 1978). The plots on Site I and Site II were fumigated for 4 years (1975–1978) and 3 years (1976–1978), respectively. Sulfur dioxide was blended with air and dispensed through a network of aluminum pipes located approximately 0.75 m above ground surface. Canopy-level concentrations of SO_2 were determined hourly (for 7.5-min periods) with a Meloy Laboratories (Model SA 160-2) sulfur analyzer. SO_2 was delivered to each plot at a constant rate; therefore, temporal variations in SO_2 concentration varied with environmental conditions, especially wind speed. Preston and Gullett (1978) found hourly concentrations were log-normally distributed and decreased with height in the canopy. Concentrations at 15 cm height in the canopy were 75% of those at canopy height (30 cm) and, although not measured, were presumed to be even less at ground level. Nighttime concentrations were nearly twice as great as daytime concentrations. Details of the fumigation system are presented by Lee and Lewis (1978).

Precipitation was measured on each study site between May and September in each year. Soil water content to a depth of 105 cm was determined gravimetrically on each treatment plot throughout each growing season. Sampling frequency varied from weekly to monthly during the study.

Aboveground plant biomass was sampled on six dates in 1975 and 1976, in mid-July in 1977 and in mid-May and mid-July in 1978. Quadrats were located randomly, and vegetation was clipped at the soil surface and separated by species into current live, recent dead (current year's dead) and old dead (previous year's dead). Samples were oven dried at 60° C to constant weight and weighed. In 1975, ten circular 0.5-m^2 quadrats were sampled in each treatment on each date. This was changed to 20 circular 0.25-m^2 quadrats in 1976, 1977, and 1978 to increase precision.

Although numerous computational procedures exist for estimating ANPP from harvest data (Singh et al. 1975), only one procedure was appropriate for all treatments in all years of this study: the total standing crop of current production as measured in mid-July. The more accurate procedure summing species and species group peaks of current production from frequent harvest data could be used only in 1975 and 1976, when we sampled monthly throughout the growing season. We computed ANPP estimates by both procedures for 1975 and 1976. The summation of peaks procedure resulted in an 18% (SE = 3%) greater estimate of ANPP than did the July standing crop estimate. A comparable difference between the two procedures was reported for a South Dakota grassland of similar botanical character (Dodd et al. 1974). Therefore, our estimates of ANPP are July standing crop estimates increased by 18%.

Belowground plant biomass to a depth of 10 cm was sampled monthly (May–September) in 1975, 1976, and 1978 and in mid-July in 1977. Lauenroth et al. (1975) and Dodd et al. (1974) have reported that approximately 50% of the belowground plant biomass is located in the 0–10 cm layer of the rooting profile. On each sampling date 2 belowground samples were taken from each harvested quadrat location after harvest of the aboveground material. Samples were secured with a 7.5 cm diameter × 10 cm long steel cylinder. Plant material was separated from soil by the washing-flotation procedure described by Lauenroth and Whitman (1971) and separated into roots, rhizomes, and crowns (basal parts of shoots that are subterranean but positioned above the transition zone of the plant). This washing-flotation procedure retains all live and dead belowground plant material that will not pass through a 60-mesh $\cdot$ in^{-1} screen. Separated materials were oven-dried to a constant weight, ashed at 600° C, and reweighed; results are reported on an ash-free basis.

Separate statistical analyses were performed on data sets within each Site (I and II). Two-way analyses of variance were conducted on each data set. Tukey's Q procedure was used to compute range values for comparison of means (Sokal and Rohlf 1969).

Results and Discussion

Precipitation and Soil Water

Early growing season precipitation (May–July) was near normal in 1977, 40% greater than normal in 1975, and more than twice normal in 1978 (Table 1). Although early season precipitation in 1976 was nearly 40% above normal on Site, I it was only slightly above normal on Site II. August and September precipitation was low and near normal in all years. Soil water storage was high in early season and rapidly depleted in July and August in all years (Fig. 1).

Aboveground Biomass Dynamics

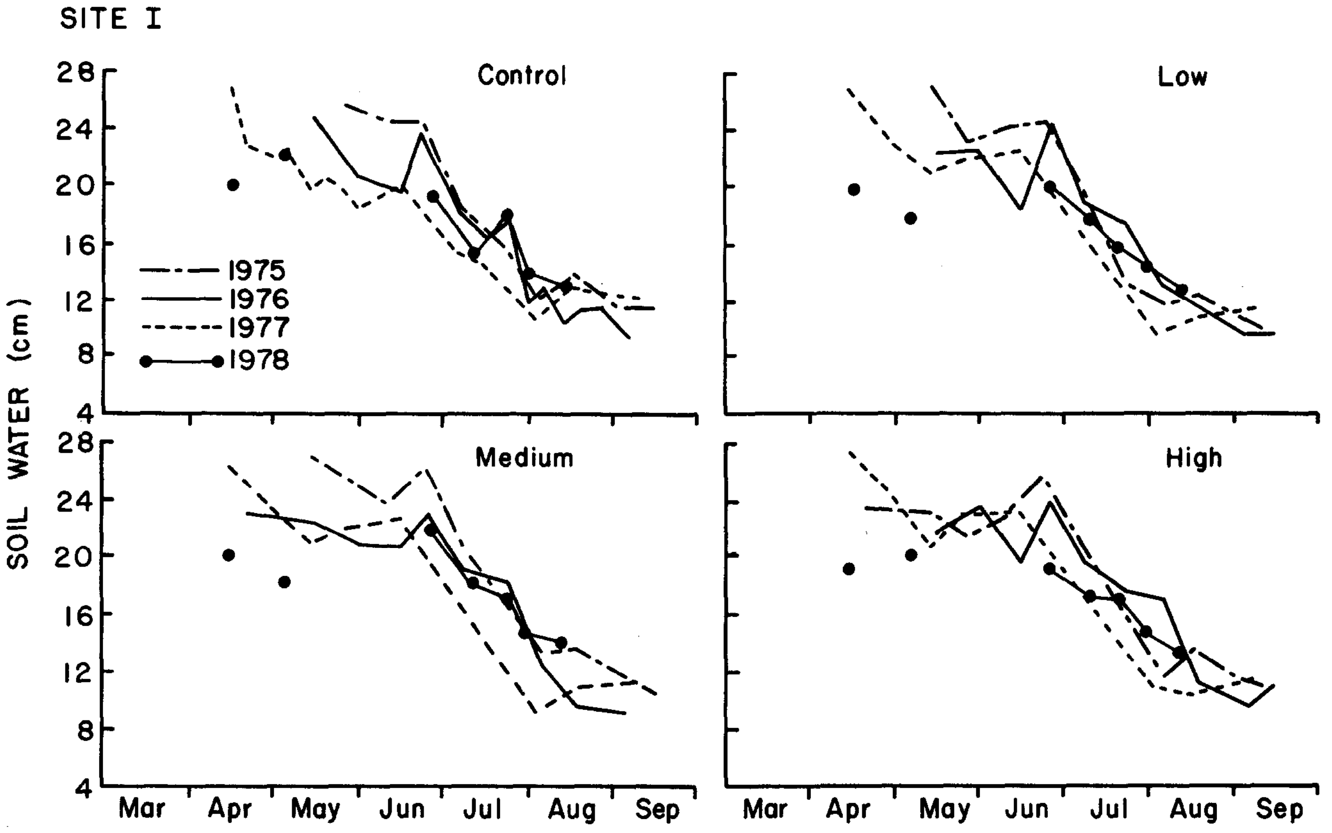
In 1975 and 1976 seasonal biomass dynamics for the total plant community consisted of an early period of rapid increase (late April to early July), followed by a period of slight increase (1975) or a slight decrease (1976) in standing crop of current seasons production (Fig. 2). The cessation of rapid growth was associated with diminished rainfall and rapid exhaustion of soil water (Fig. 1). The SO_2 treatments did not alter the timing or rates of standing crop increases during the rapid growth period, nor did the treatment alter the post-peak biomass dynamics.

Community biomass dynamics were largely a reflection of the biomass dynamics of western wheatgrass (Fig. 3) and to a lesser extent of prairie junegrass (Fig. 4). Although the low frequency of

Table 1. Growing season precipitation (mm) for Sites I and II, 1975–1978, compared with long-term average (1932–1977) at Broadus, Montana.[1]

	1975 Site	1976 Site		1977 Site		1978 Site		
Month	I	I	II	I	II	I	II	Long-term average
May	104	97	44	45	46	263	276	57
June	109	102	94	91	98	57	56	80
July	29	38	41	18	14	28	30	35
August	14	10	17	18	18	13	11	27
September	6	14	14	36	40	No data		30
May-July	242	237	179	154	158	348	362	172

[1] Broadus, Montana, is located 40 km northeast of the study sites.



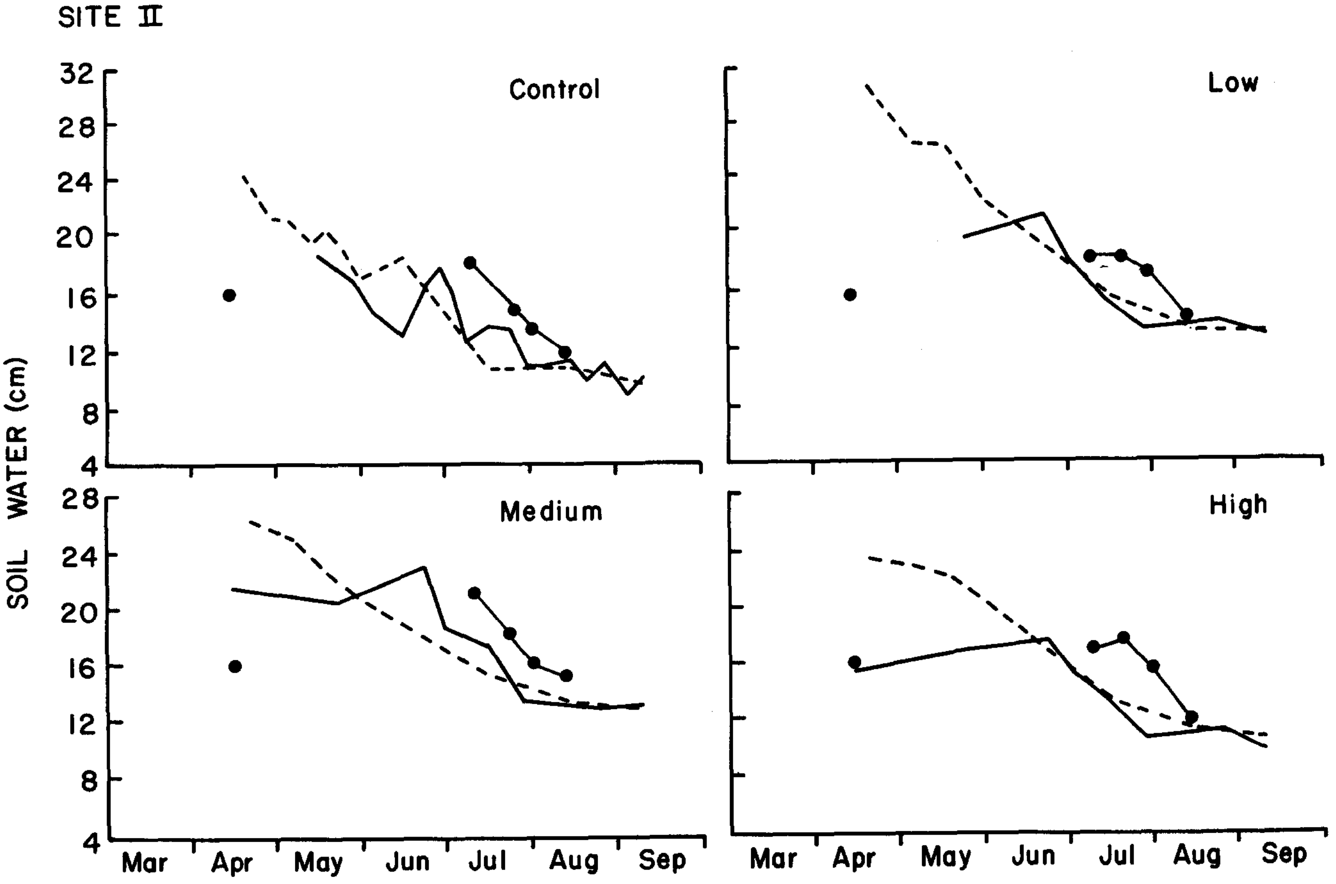


Fig. 1. *Soil water dynamics within 0-105 cm depth for Sites I and II, 1975-1978.*

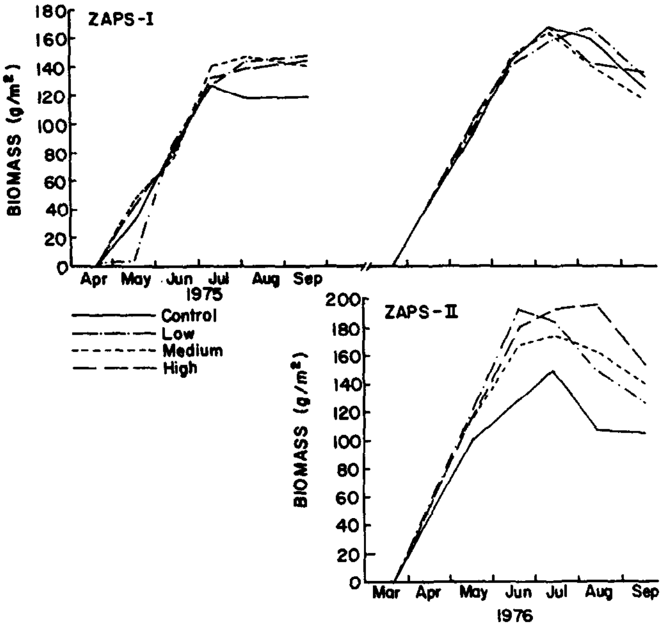


Fig. 2. *Seasonal change in current year's production for all plant species combined, ZAPS, I AND II, 1975 and 1976.*

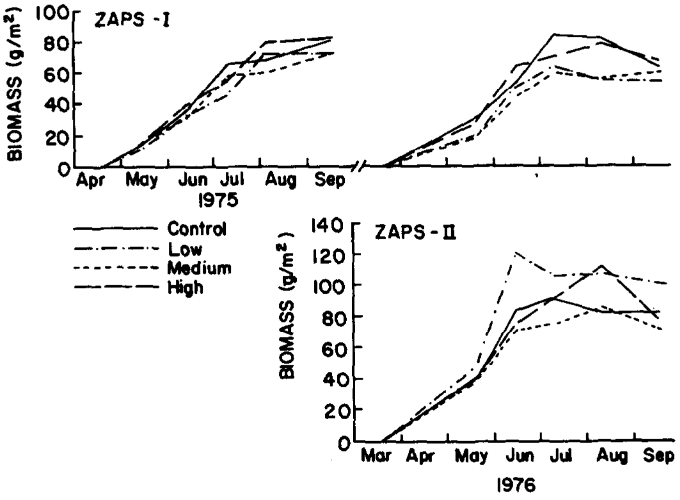


Fig. 3. *Seasonal change in current year's production for western wheatgrass, ZAPS I and II, 1975 and 1976.*

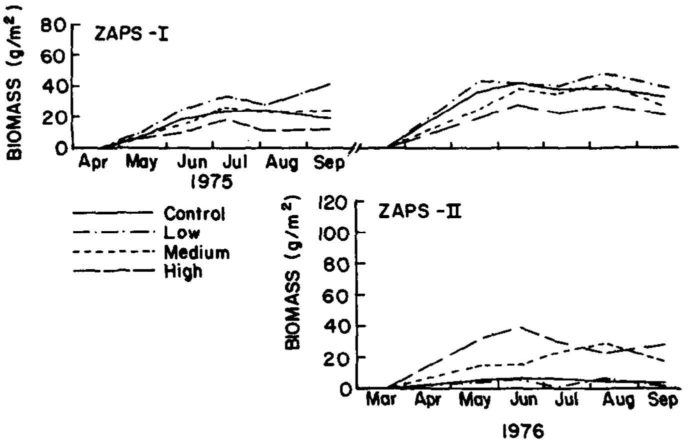


Fig. 4. *Seasonal change in current year's production for prairie junegrass, ZAPS I AND II, 1975 and 1976.*

standing crop estimates prohibits precise evaluation, western wheatgrass appeared to have its most rapid aboveground growth period later in the season than did prairie junegrass. Also, western wheatgrass standing crop persisted longer after the rapid growth period than did prairie junegrass. Treatment induced changes in biomass dynamics of these two species were not detected.

The effects of weather (year) and SO_2 treatment on interseasonal dynamics of aboveground biomass production are shown in Tables 2 and 3. With the exception of species groups containing *Bromus japonicus* on Site II, weather fluctuations and SO_2 treatments did not affect production in an interactive manner.

In general, production of all major species and species groups was less on Site I than on Site II. Production for most groups on both study sites was least in 1977, the driest year studied, and was greatest in 1976 (Site 1) or 1978 (Site II).

Production for both sites was dominated by cool-season peren-

Table 2. Annual variation in July standing crop (g • m^{-2}) of current production for Sites I and II (Averages of control and three SO_2 treatments).[1]

	Site I				Site II		
	1975	1976	1977	1978	1976	1977	1978
Cool-season grasses							
Agropyron smithii	56^{bc2}	69^{c}	39^{a}	48^{ab}	91^{a}	92^{a}	119^{b}
Bromus japonicus	1^{a}	3^{a}	1^{a}	2^{a}	9	6	26
Koeleria cristata	26^{ab}	35^{b}	21^{a}	21^{a}	15^{a}	11^{a}	18^{a}
Poa spp.	2^{a}	5^{a}	2^{a}	5^{a}	30^{b}	11^{a}	15^{ab}
Stipa comata	9^{a}	5^{a}	6^{a}	5^{a}	+	+	+
Stipa viridula	+	+	+	+	7^{a}	5^{a}	8^{a}
Other CSG	8^{a}	3^{a}	7^{a}	4	$+^{a}$	1^{a}	2^{a}
Total[3]	98^{b}	116^{c}	73^{a}	82^{a}	143^{a}	120^{a}	162^{b}
Cool-season forbs							
Achillea millifolium	6^{a}	11^{a}	7^{a}	6^{a}	6^{a}	4^{a}	1^{a}
Tragopogon dubius	6^{a}	13^{a}	13^{a}	11^{a}	3^{a}	4^{a}	5^{a}
Taraxacum officinale	3^{a}	7^{ab}	2^{a}	$+^{a}$	10^{b}	9^{b}	1^{a}
Other CSF	8^{a}	5^{a}	5^{a}	7^{a}	2^{a}	2^{a}	2^{a}
Total cool-season forbs	23^{a}	36^{a}	27^{a}	24^{a}	21^{b}	19^{b}	9^{a}
Other plants	9^{a}	10^{a}	7^{a}	7^{a}	3^{a}	5^{a}	5^{a}
Total current production[3]	131^{b}	165^{c}	107^{a}	115^{a}	166^{b}	143^{a}	176^{b}

[1] Means within rows and sites not followed by the same letter are significantly different ($P = .05$).

[2] Year × treatment interactions were significant ($P < .05$), see Figure 5.

[3] This total does not include *B. japonicus.*

Table 3. Effect of three levels of SO_2 fumigation on July standing crop ($g \bullet m^{-3}$) of current production for Sites I and II (Averages for 1975-1978 and 1976-1978, respectively).

	Site I				Site II			
	Cont.	Low	Med.	High	Cont.	Low	Med.	High
Cool-season grasses								
Agropyron smithii	60^{a}	49^{a}	48^{a}	55^{a}	95^{ab}	124^{c}	79^{a}	105^{bc}
Bromus japonicus	4^{a}	1^{a}	1^{a}	$+^{a}$	30[1]	14[2]	8[2]	3[2]
Koeleria cristata	25^{a}	30^{a}	29^{a}	19^{a}	5^{ab}	2^{a}	22^{bc}	32^{c}
Poa spp.	2^{a}	4^{a}	4^{a}	3^{a}	12^{a}	19^{a}	23^{a}	22^{a}
Stipa comata	5^{ab}	11^{b}	7^{ab}	1^{a}	+	+	+	+
Stipa viridula	+	+	+	+	6^{a}	2^{a}	10^{a}	10^{a}
Other CS	3^{a}	7^{a}	8^{a}	1^{a}	+	1	+	+
Total[3]	94^{b}	101^{b}	96^{b}	79^{a}	117^{a}	148^{bc}	134^{ab}	168^{c}
Cool-season forbs								
Achillea millifolium	8^{a}	2^{a}	4^{a}	17^{b}	1^{a}	6^{a}	2^{a}	5^{a}
Tragopogon dubius	10^{a}	13^{a}	12^{a}	7^{a}	5^{a}	1^{a}	5^{a}	4^{a}
Taraxacum officinale	2^{a}	1^{a}	4^{a}	6^{a}	4^{a}	12^{b}	8^{ab}	3^{a}
Other CSF	5^{a}	7^{a}	7^{a}	6^{a}	3^{a}	1^{a}	3^{a}	1^{a}
Total cool-season forbs	25^{a}	23^{a}	27^{a}	36^{a}	14^{a}	20^{a}	19^{a}	13^{a}
Other plants	6^{a}	6^{a}	6^{a}	13^{a}	3^{a}	2^{a}	6^{a}	6^{a}
Total current[3] production	125^{a}	131^{a}	129^{a}	128^{a}	135^{a}	169^{bc}	158^{b}	186^{c}

[1] Means within rows and sites not followed by the same letter are significantly different ($P = .05$).

[2] Year × treatment interactions were significant ($P < .05$), see Figure 5.

[3] This total does not include *B. japonicus*.

nial grasses with *Agropyron smithii* the most productive species of the group. The major secondary grass species on Site I was *Koeleria cristata*, while on Site II *Bromus japonicus* and *Poa* spp. were also important secondary grass components. Although cool-season forbs were a consistent component of the plant community on both study sites, the group was much less productive than the grasses and exhibited very little annual variation.

The effects of SO_2 on biomass production were not dramatic (Table 3). On Site I, *Stipa comata,* a cool-season perennial bunch grass, had greater production on the low SO_2 treatment than on the high SO_2 treatment suggesting a stimulation by SO_2 at the low level of exposure and an inhibition at the high level of exposure. However, no other significant responses were noted on Site I. On Site II, *Agropyron smithii* and *Taraxicum officinale,* both showed some evidence of stimulation in production at the low and medium exposure levels, respectively, while *Koeleria cristata* production was increased on the medium and high treatment. The lack of consistency in trend of response on the two test sites suggests that these differences may reflect differences in the treatment plots which existed prior to application of the SO_2 treatments rather than resulted from the treatments.

Bromus japonicus is a cool-season winter annual grass and its annual production is thus highly variable and dependent upon timing of available soil water during fall and early spring (Hyder et al. 1975). Production of *B. japonicus* was consistently low and did not respond to the SO_2 treatments on Site I (Table 3). However, on Site II, production of this species was higher than on Site I and was significantly depressed by the SO_2 treatments in 1978 and possibly 1977 (Fig. 5). It is likely that production of this species was depressed by SO_2 on both study sites during each year of the experiment, but the differences were masked by sampling error during years of low production. During 1978 the production (y) of this species decreased exponentially with seasonal geometric mean concentration of SO_2 (x), [$y = 72^{-.47x}$, ($R^2 = .75$)].

Explanation for the inhibitory effect of SO_2 on production of *B. japonicus* and not on *Agropyron smithii* may be associated with differential sulfur uptake rates by the two species. Gordon et al. (1978), working on the SO_2 treatments of Site I in 1975, reported sulfur accumulation rates for *B. japonicus* that were nearly double those for *A. smithii.* It is generally accepted that physiological injury induced by SO_2 derivatives is directly related to SO_2 uptake rates and that uptake of SO_2 increases with transpiration intensity and stomatal opening (Ziegler 1975, Winner and Mooney 1980). The higher uptake of SO_2 by *B. japonicus* probably resulted from a stimulation of stomatal opening by SO_2 (Ziegler 1975), or may simply reflect higher intrinsic conductance rates for *B. japonicus* than for *A. smithii.* We have conducted laboratory studies (unpublished) which indicate that 1-hour exposures of *A. smithii* to low levels of SO_2 (500–2,000 $\mu g \bullet m^{-3}$) under a wide range of relative humidities consistently results in decreased transpiration and CO_2 uptake. Related work on these species (Lauenroth and Dodd in prep.) indicates that *B. japonicus* experienced much more chlorophyll destruction in our field exposure experiment than did *A. smithii.*

Aboveground Net Primary Production (ANPP)

ANPP was not estimated for the test sites before exposure to

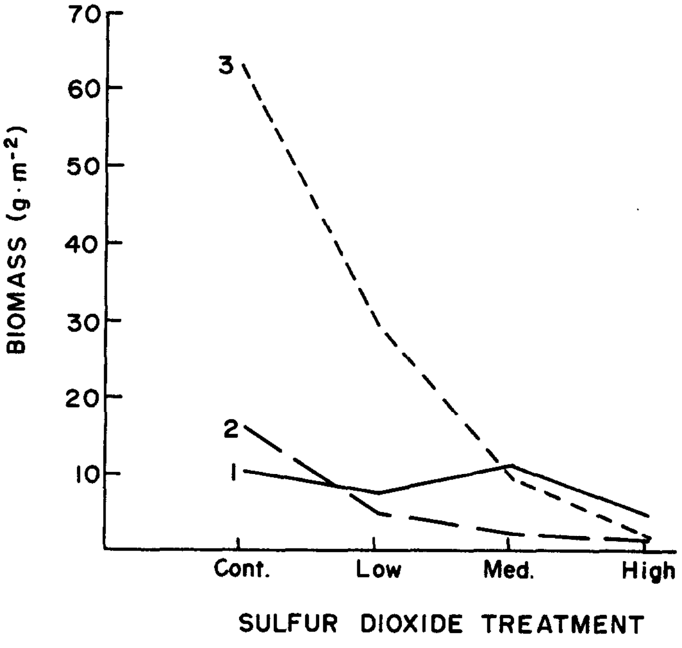


Fig. 5. *Interseasonal biomass dynamics for* Bromus japonicus *on control and three SO_2 treatments. (1 = 1976; 2 = 1977; 3 = 1978). Means that differ by > 41 g are significantly different* ($P = .05$).

SO_2. Therefore, our assumption that the treatment areas within each of the test sites were equal in production potential to the control areas before fumigation can only be tested with less appropriate information. Standing crop residual from annual production occurring in the year preceding fumigation was determined in the spring of the first season of exposure and indicates only slight differences among the control and treatment areas on either site (Table 4). The low and medium areas on Site I had slightly higher residual material than did the control and high areas. And on Site II the residual material was slightly greater on the control than on the treatment areas. Since slight differences in residuals could also arise from differential weathering associated with drifted snow during the winter months we conclude that the residual estimates indicate slight, if any, differences in production potential within either test site.

Table 4. Residual standing crop ($g \bullet m^{-2}$) of previous years aboveground production for Site I and Site II in spring before first season of SO_2 treatment.

	Control	Low	Medium	High
Site I, April 1975	77 ± 7[1]	97 ± 8	93 ± 7	81 ± 10
Site II, March 1976	86 ± 4	75 ± 6	66 ± 6	64 ± 4

[1] $X \pm SE$, $g \bullet m^{-2}$

ANPP ranged from 119 to 268 $g \bullet m^{-2}$ throughout the study period and Site II was more productive than Site I (Table 5). The greatest differences in ANPP were between years. While 1977, the driest year of the study (Table 1), was clearly the least productive year on both sites, 1978, the wettest year, was the most productive only on Site II. In fact, ANPP in 1978 on Site I was not significantly greater than in 1977 and was lower than ANPP in 1975 and 1976. Since most of the increase in precipitation in 1978 arose from May precipitation being nearly 5 times normal (with 130 mm on May 20), we conclude that this amount was excessive and reduced productivity via leaching of required nutrients on Site I. Since ANPP was not similarly depressed on Site II, we suggest that nutrients were not leached beyond the effective rooting zone because of differences in soil characteristics. Clay contents in the upper 30 cm of the profile range from 33 to 42% on Site II and from 16 to 32% on Site I (Dodd et al. 1978). Fertility factors associated with these textural differences between Site I and Site II are also presumed to account for the differential productivity noted between Sites I and II.

Treatment differences in ANPP were not detected on Site I. And, although statistically significant treatment differences were noted on Site II, the patterns of the differences are not suggestive of responses to SO_2 exposure but instead reflect spatial variability within the study site.

Belowground Biomass Dynamics

Belowground plant biomass dynamics were dominated by changes in root biomass. Even though root standing crops were estimated monthly during the growing season on all treatments in 1975, 1976, and 1978, we found consistent intraseasonal dynamics only in 1978 (Table 6). From May to July, root biomass decreased by about 25% and from July to September increased by about the same amount. This demonstration of a mid-season low is generally consistent with findings of other studies conducted in the northern mixed grass prairie (Lauenroth and Whitman 1977, Dodd et al.

Table 5. Aboveground net primary production[1] for Sites I and II, 1975–1978[2].

	ZAPS I				ZAPS II			
	Control	Low	Medium	High	Control	Low	Medium	High
Year	$X \pm SE$	$X \pm SE$	$X \pm SE$	$X \pm SE$	$X \pm SE$	$X \pm SE$	$X \pm SE$	$X \pm SE$
1975	150±14	149±17	165±13	156±14				
1976	199±13	186± 9	195±11	199± 8	177± 8	218±17	205±14	227±15
1977	126±12	131±13	131± 7	119± 5	137± 7	210±13	169± 9	190±11
1978	136± 8	156±14	123± 6	129± 6	268±18	219±18	214±13	253± 8

[1] $g \bullet m^{-2}$.
[2] ANPP = July current production × 1.18.

Table 6. Seasonal root biomass dynamics for Sites I and II, 1978.

	Site I				Site II			
Date	Control	Low	Medium	High	Control	Low	Medium	High
20 May 1978	709±27[1]	732±28	759±31	822±38	613±43	766±28	688±34	791±33
20 July 1978	650±50	614±26	624±24	737±41	643±25	755±38	624±34	608±29
17 July 1978	549±30	501±27	521±20	491±16	649±27	585±35	546±43	434±22
16 August 1978	598±35	713±42	741±44	720±32	738±33	765±44	827±37	708±27
15 September 1978	709±37	771±43	724±31	801±29	646±33	795±46	788±35	665±38
Average	643	676	674	714	658	733	695	641

[1] $X \pm SE$, $g \bullet m^{-2}$, ash-free biomass, 0–10 cm depth.

Table 7. Average standing crop ($g \bullet m^{-2}$) of belowground biomass by morphological categories (0–10 cm depth), Site I, 1975–1978.

	Year			SO_2 Treatment			
	1975	1976	1978	Cont.	Low	Med.	High
Crown	51^a	70^b	97^c	74^a	77^a	74^a	66^a
Rhizome	25^a	32^b	30^b	37^b	26^a	27^a	26^a
Roots	549^a	528^a	677^b	586^a	573^a	582^a	596^a
Total	624^a	629^a	803^b	697^a	676^a	682^a	687^a

[1] Means within a row for each year or treatment set not followed by the same letter are significantly different ($P = .05$).

Table 8. Average standing crop (g • m^{-2}) of belowground biomass by morphological categories (0-10 cm, in depth), Site II, 1976, 1978.

	Year		SO$_2$ Treatment			
	1976	1978	Cont.	Low	Med.	High
Crowns	71^{a}	99^{b}	79^{a}	88^{a}	84^{a}	88^{a}
Rhizomes	28^{a}	32^{b}	26^{a}	35^{b}	31^{ab}	29^{a}
Roots	593^{a}	682^{b}	593^{a}	669^{a}	661^{a}	626^{a}
Total	692^{a}	813^{b}	697^{a}	791^{a}	775^{a}	744^{a}

[1] Means within a row for each year or treatment set not followed by the same letter are significantly different ($P = .05$).

1974, Lewis et al. 1971) and simulations of belowground dynamics (Bartos and Jameson 1974, Detling et al. 1979). The SO$_2$ treatments did not alter seasonal changes in root biomass in 1978.

Average seasonal biomass of all belowground plant categories increased from 1975 to 1978 on Site I (Table 7), and from 1976 to 1978 on Site II (Table 8). This was apparently in response to removal of grazing pressure or to more favorable weather during the study period than in preceding years (weather records not available from study sites prior to 1975).

Crown and root components of belowground biomass were not changed by the SO$_2$ treatments. However, on Site I rhizomes were significantly reduced on all SO$_2$ treatments. On Site II rhizomes were slightly increased by the low SO$_2$ treatment and unchanged by the medium and high treatments. We have no explanation for the differential response of rhizome biomass to SO$_2$ between Site I and Site II. Although the interactive effects of SO$_2$ treatment and year on rhizome biomass were tested for and found not to be significant ($P > .10$), rhizome growth between the first year of exposure and 1978 appeared to be inhibited by the SO$_2$ treatments. By 1978 rhizome biomass had increased by 30%, 20%, 10%, and less than 10% on the control, low, medium, and high treatments, respectively, on both study sites (Table 9).

Conclusions

Aboveground total plant biomass dynamics, aboveground total net primary productivity, and total belowground biomass dynamics of northern mixed grass prairie are not immediately sensitive to low level SO$_2$ exposure regimes. However, short-term reductions in rhizome biomass suggest that aboveground biomass dynamics and primary productivity may eventually be altered because of loss of capability of rhizomes to support aboveground processes in western wheatgrass, the dominant plant species in this grassland type. Production of *Bromus japonicus* was significantly decreased by SO$_2$ in one season. We assume that similar disruptions of carbon capture and/or allocation to storage organs of other plant species may also occur and could ultimately contribute to significant changes in primary productivity, biomass dynamics, and species composition.

Concentrations of SO$_2$ utilized in this study were greater than those expected in the vicinity of any single power plant, extant or proposed, for the Northern Great Plains (Duran et al. 1979). Our treatments represent conditions which may result from a large number of coal consuming installations in a region such as southeastern Montana and northeastern Wyoming. Our treatment concentrations bracket federal standards and therefore provide information about the short-term validity of the current standards and a preview of responses which may be expected if standards are relaxed.

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Table 9. Seasonal average rhizome biomass for control and SO$_2$ treatments, Sites I and II, 1975–1978.[1]

	Site I				Site II			
Year	Control	Low	Medium	High	Control	Low	Medium	High
1975	29	22	25	24				
1976	42	30	29	29	23	32	28	29
1978	39	27	28	26	29	37	32	30

[1] g • m^{-2} ash-free, 0–10 cm depth.

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